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SEVEN YEAR POST-FIRE REGENERATION PATTERNS OF WHITEBACK PINE IN THE GREATER YELLOWSTONE AREA

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Patterns of Post-fire Regeneration of Whitebark Pine in the Greater Yellowstone Area

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CONE PRODUCTION, MOISTURE, AND THE ADVANTAGE OF DELAYED SEED GERMINATION IN WHITEBARK PINE

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Abstract. Whitebark pine (*Pinus albicaulis*) seeds are dispersed by Clark's Nutcracker (*Nucifraga columbiana*). Previous experimental and field observations suggest that the seeds may experience delayed germination of two years or more. In addition, the seeds are difficult to germinate under nursery conditions because of underdeveloped embryos, profound dormancy, and a seed coat resistant to moisture uptake. From 1990 to 1995 we investigated patterns of natural whitebark pine regeneration following the 1988 Yellowstone fires to determine whether whitebark pine typically exhibits a pattern of delayed seed germination and whether delayed germination might be adaptive, possibly leading to greater recruitment rates over time. We established 275 permanent plots divided between Henderson Mountain, Gallatin National Forest, Montana, and Mt. Washburn, Yellowstone National Park. In the Henderson Mountain study area, the ecological treatments included: dry, burned; moist, burned; dry, unburned; and moist, unburned. The following treatments were established in the Mt. Washburn study area: dry, burned; moist, burned; and moist, moderately burned.

Regeneration densities were consistently highest on the Mt. Washburn moist treatments, the most mesic of all. Whitebark pine seed germination did not necessarily follow moderate to good cone crops: the greatest densities of new regeneration occurred in the summers of 1991 and 1993, but the highest cone production occurred in the late summers of 1989 and 1991. The high density of germination in 1991 and 1993 appeared to correlate with high March plus April precipitation in these years, suggesting that the characteristics of whitebark pine seeds that lead to delayed germination may establish an adaptive moisture threshold in an arid environment. Although underdeveloped embryos and endosperm may be partly the result of a short growing season and premature seed dispersal by nutcrackers, the seed caching mode of dispersal may

further select for these traits as well as moisture-resistant seed coats. These seed traits combined appear to result in 1) germination under conditions favorable to seedling survival and 2) continuity of regeneration through time, independent of cone production.

Introduction

Temperate zone forest trees live in environments that vary from year to year in favorability for both reproduction and recuitment. For some forest trees, and conifers in particular, suitable conditions are both infrequent and unpredictable. Johnson and Fryer (1996) identify three alternative strategies based on different life history stages that may be used by long-lived plants, i.e., trees, to exploit favorable conditions when they occur: 1) storage of seeds in a seed bank, either in the soil or in serotinous cones, 2) storage of individuals in a seedling bank, i.e., advanced regeneration, under the current overstory, and 3) maintenance of a long-lived overstory or bank of adult trees that produce some seeds each year. Whereas the seeds of some temperate hardwoods may delay emergence and form a seed bank for one or two years (Marquis 1975), the majority of conifers use the latter two strategies. High rates of seed predation and rapid loss of seed viability over the first year usually preclude maintenance of a seed bank, e.g., Engelmann spruce (*Picea engelmannii)* (Johnson and Fryer 1996). With respect to pines (Pinaceae, *Pinus*), the trend is similar, although there are several species whose seeds may delay germination for one to several growing seasons, e.g., jack pine (*Pinus banksiana*), eastern white pine (*P. strobus*), western white pine (*P. monticola*), Balkan pine (*P. peuce*), Swiss stone pine (*Pinus cembra*), Korean stone pine (*P. koraiensis*), and whitebark pine (*P. albicaulis*) (Haig et al. 1941, Krugman et al. 1974, Krugman and Jenkinson 1974, Thomas and Wein 1985, McCaughey 1993). These pine species may use a combination of strategies to improve recruitment through time, including forming a seed bank that responds to favorable conditions, particularly adequate moisture (Krugman et al. 1974). However, the ecological implications of delayed seed germination are virtually unknown for pines, and the evolutionary and ecological factors favoring delayed seed germination in pines

are largely unexplored.

The 1988 fires in Yellowstone National Park provided an opportunity to study patterns of post-fire seed germination in whitebark pine (*Pinus albicaulis*) on a large geographic scale and in multiple treatments. A subalpine and treeline conifer, whitebark pine ranges throughout the higher mountains of the western United States and southern Canada, including the northern Rocky Mountains, the Coast Ranges, Cascades, and Sierra Nevada Range (Arno and Hoff 1989). In the northern Rocky mountains and the Greater Yellowstone Area, whitebark pine forms climax communities on high elevation or exposed sites and successional communities on favorable sites. The seral communities are renewed by fire every 50 to 400 years (depending on the region); in the absence of fire, whitebark pine is gradually replaced by shade-tolerant conifers, particularly subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmanni*) (Arno 1980, 1986, Romme 1982, Arno and Petersen 1983, Keane et al. 1990, Barrett 1994).

Whitebark pine is the only North American species of the holarctic, bird-dispersed pine subsection *Cembrae*. This subsection contains five species (Critchfield and Little 1966), all dependent on nutcrackers (*Nucifraga* spp.) for seed dispersal; all *Cembrae* pines have large, wingless seeds and indehiscent cones, i.e., the cone scales separate only slightly from the core when the seeds are ripe (Lanner 1990). Whitebark pine seeds are primarily dispersed by Clark's Nutcrackers (*N. columbiana*), which harvest seeds from cones in late summer and fall and may transport 100 or more whitebark pine seeds at a time in their sublingual pouch to storage areas (Tomback 1978, 1982, Hutchins and Lanner 1982). Nutcrackers typically bury caches of 1 to 15 seeds (with a mean of 3 or 4 seeds) under 2 to 3 cm of soil (Tomback and Linhart 1990). These caches provide food for nutcrackers and their young until the next cone crop, but unretrieved

caches may germinate in late spring and summer, producing clusters of seedlings (for a review of Clark's Nutcracker behavior and ecology, Tomback 1997).

Two studies indicate that whitebark pine seeds are capable of delaying germination, i.e., they do not always germinate in the growing season following dispersal: McCaughey (1993) hand-sowed individual whitebark pine seeds 2 to 4 cm below soil into several experimental treatments in a subalpine zone clearcut and found that 11% of the seeds germinated in the first year, 45% in the second year, and and 11% in the third year. Small numbers of seeds continued to germinate in subsequent years (McCaughey, *personal communication*). Tomback et al. (1993), working in two burns in western Montana, found that within about 65 to 85 % of naturally-regenerated whitebark pine seedling clusters (each cluster presumably from a single caching event), seedlings differed in age by 1 to 8 years with most age differences of 1 to 3 years.

Recently-harvested whitebark pine seeds are notoriously difficult to germinate in the laboratory, requiring long or compound stratification and clipping or removal of seed coats or treatment with sulfuric acid to weaken seed coats (Pitel and Wang 1980, 1990, Leadem 1985). The same factors that account for low germination success probably result in delayed germination under natural conditions: 1) many seeds in ripe cones contain underdeveloped embryos and endosperm (actually, female gametophyte), although there appears to be some variation among populations in this trait (e.g., Pitel and Wang 1990); 2) long stratification periods are necessary to break seed dormancy, indicating a physiological state resistant to germination; and 3) the seed coat may be resistant to water uptake and/or impose some mechanical restraint to embryo expansion (Pitel and Wang 1980, 1990, Leadem 1986). Leadem (1986) suggested that these seed traits were adaptive for whitebark pine, leading to germination under favorable conditions.

From 1990 to 1995 we investigated patterns of natural whitebark pine regeneration following the 1988 Yellowstone fires to determine whether whitebark pine typically exhibits a pattern of delayed seed germination under natural (non-manipulated) conditions and to examine whether delayed germination might be adaptive, possibly leading to relatively greater recruitment rates over time. Specifically, we predicted that delayed germination typically occurs in whitebark pine if the highest densities of new seedlings do not necessarily follow good or moderate cone production the previous fall, i.e., if new regeneration was asynchronous with seed production. Secondly, if indeed delayed germination occurred, we predicted that high moisture availability, either as average snowpack, cumulative precipitation, or pre-growing season (March and April) precipitation triggered germination in dormant seeds. Thirdly, if dormant seeds germinate in response to moist conditions, we predict that delayed germination leads to greater survivorship of seedlings.

Methods

Study areas

In 1990 we established a total of 275 permanent plots divided between two subalpine forest study areas in the Greater Yellowstone Ecosystem that had been burned during the 1988 Yellowstone fires. Prior to fire, the forests in both study areas consisted of successionally advanced whitebark pine communities, dominated by subalpine fir and Engelmann spruce. The Henderson Mountain study area is about 3 km straightline distance northeast of Cooke City, Montana, on south- and east-facing slopes of Henderson Mountain in the Fisher Creek drainage of the Beartooth Mountains, Gallatin National Forest; the study area ranges from about 5 to 7 km from the northeast boundary of Yellowstone National Park (Fig. 1). Part of Henderson

Mountain and vicinity experienced severe, stand-replacing fire in 1988 from a backburn set by firefighters to protect Cooke City from the Storm Creek Fire. The nearest unburned whitebark pine stands that are potential seed sources occur adjacent to the burned areas in unburned treatments and just above the study area on Henderson Mountain in climax stands of mixed conifers. The soils in this area are in transition between sedimentary, limestone, and glacial till. They are moderately coarse to medium textured with many coarse fragments, well-drained, but of low fertility (H. Shovic, *personal communication*).

The Mt. Washburn study area lies in the northcentral region of Yellowstone National Park, ranging from 7 to 9 km north of Canyon Junction, on the north and west slopes of Mt. Washburn (Fig. 1). Much of the subalpine forest on the western slope faces of Mt. Washburn was burned in a mosaic pattern by the North Fork Fire. Fire severity in this area varied from severe, stand-replacing fire to moderate canopy fire and surface fire, which left many trees alive. Unburned seral whitebark pine stands among the treatments in the Mt. Washburn study area and climax stands on the upper elevations of Mt. Washburn, just above the treatments established for this study, provide potential whitebark pine seed sources. The soils in this area are of moderately coarse texture and developed in shallow, glacial till from andesitic rocks. They are extremely well-drained, variable in depth, and moderate in fertility (H. Shovic, *personal communication*). Whereas lodgepole pine (*Pinus contorta*) was a minor component of the pre-fire forest in the Henderson Mountain study area, it was an important conifer in the Mt. Washburn study area pre-fire forest (Fig. 2 and 3).

Study design

The study design consisted of seven ecological treatments with 25 to 50 circular plots,

each 20 m^2 in area, per treatment (Table 1). The center of each plot was marked by a numbered rebar stake painted orange. Plot perimeters were reconstructed once each summer, as needed, with a radius line of fixed length (2.52 m) and circumference marked with surveyor's flags. We established four different ecological treatments in the Henderson Mountain study area: 1) dry, burned 2) moist, burned, 3) dry, unburned, and 4) moist, unburned. In the Mt. Washburn study area, we established three ecological treatments: 1) dry, burned, 2) moist, burned, and 3) moist, moderately burned. All "burned" treatments experienced stand-replacing fire with no surviving trees. The "moderately burned" treatment experienced a spotty surface fire that spared part of the canopy and some of the understory. Whereas in the "burned" treatments all substrate organic material was consumed, leaving mineral soil and ash, in the "moderately burned" treatment a litter layer of dead conifer foliage built up rapidly.

The distinction between dry and moist ecological treatments was based on whether or not moist site herbaceous plant indicators were present in the understory and in adjacent meadows and, most importantly, on the presence or absence of Engelmann spruce as a dominant in the pre-fire forest. In the Henderson Mountain study area, the moist treatments were adjacent to a spring-fed meadow. On Mt. Washburn, the moist treatments corresponded to northerly slope aspects. We quantified differences in conifer composition in the pre-fire forest in order to corroborate our treatment assignments; in each treatment, we surveyed 1 or 2 quadrats, 30 by 30 m in area, selected at random. Within each quadrat, we assigned every tree and sapling to a species based on tree architecture and burned bark characteristics or to "unknown" if not identifiable; we also counted fallen trees but did not count obvious clonal growth or seedlings below 15 cm in height.

All plots were surveyed for regeneration from about 12 July through 10 August each year from 1990 through 1992, and again in 1994. Since the majority of whitebark pine regeneration occurs from mid-June to the end of July (McCaughey 1990), we saw most of the regeneration in our surveys. In 1995, the final year of the study, fieldwork began on 1 August and ended about 1 September to ensure that the majority of regeneration was, in fact, recorded. During plot surveys, a minimum of two people slowly and thoroughly searched a plot area for whitebark pine germinants of the year and older regeneration; thoroughness became particularly important as density of the herbaceous vegetation increased through time. A single whitebark pine seedling or cluster of seedlings arising from a multi-seed cache was designated as a single "seedling" site and assigned an identification number. All seedlings were aged, either by known year of germination or by morphology. Occasionally, we would encounter seedlings that germinated after our survey the previous year and would assign the appropriate age and identification number. Each whitebark pine seedling site was mapped by distance and heading (compass direction) from the plot center (rebar stake) and followed from year to year; plots were carefully searched until all regeneration on sites from the previous year were either relocated or noted as missing. In 1994 we attempted to reconstruct the regeneration for 1993, the year we were not in the field. Since the orginal size of the 1993 cohort was unknown, these data are considered estimates. For data analysis, regeneration is reported as a density value, obtained by dividing the number of whitebark pine seedling sites per plot by 20 m^2. We estimated total regeneration density for each year of study by combining all seedling sites noted in the survey for that year with the few additional seedlings picked up in the subsequent survey(s). We should note that these regeneration densities err on the conservative side, because a few seedlings may germinate and die after we

complete one survey but before we complete the next.

Cone production and precipitation data

We obtained data on whitebark pine cone production for our study areas from the Interagency Grizzly Bear Study Team (National Biological Service, U. S. Department of the Interior). Each summer, the Study Team counts cones on the same 10 trees on the Republic Creek transect, which is roughly 8 km south of Henderson Mountain in the Republic Creek drainage, and on 10 trees on each of two Mt. Washburn transects. The elevations of the three transects are similar to those of the study areas, ranging from about 2650 to 2740 m. Among the three transects, the size distributions (diameter at breast height) of tagged trees are similar, as indicated by means (and standard deveiations): Republic Creek, 37.2 cm (9.7); Mt. Washburn Transect 1, 36.6 cm (13.8); and Mt. Washburn Transect 2, 33.8 cm (11.2). The size distributions do not differ significantly (Kruskal-Wallis One-way ANOVA, $H = 0.777$, $df = 2$, $P = 0.678$).

We obtained data on daily precipitation and snow accumulation for the years of this study from the Fisher Creek SNOTEL station, elevation 2774 m, which lies within 1 km of the Henderson Mountain study area. The SNOTEL automatically converts frozen precipitation to wet to provide data on cumulative precipation through time, as well as snow depth measurements. We also obtained daily weather records of frozen and wet precipitation and snow accumulation from the Tower Ranger Station at Tower Junction in Yellowstone National Park, elevation 1951 m. This was the nearest weather station to our Mt. Washburn study area, which lies about 18 km south. Because the data are collected differently at these two weather stations, they are not directly comparable but serve to indicate year-to-year trends; we converted all data to metric units.

From the Fisher Creek SNOTEL data for 1990 through 1995, we calculated total monthly and total annual precipitation, mean monthly snow accumulation (October through June), mean snow accumulation for March and April, and March plus April precipitation. From the Tower Ranger Station data for 1990 through 1995, we calculated March plus April frozen plus wet precipitation, mean monthly snow accumulation for October through April, and mean snow accumulation for March and April.

Statistical analysis

Statistical analyses were performed with either Statgraphics Plus (Version 1, Manugistics) or StatMost (DataMost Corp.) software. For each ecological treatment, we organized whitebark pine regeneration by year of germination and calculated new seedling densities. We also calculated the density of old regeneration (seedlings 1 yr of age and older) for each ecological treatment in 1995. Many plots contained no whitebark pine seedlings. We normalized densities for parametric statistical analysis by adding 1×10^{-5} to density values and taking the square root of the resulting number. Old regeneration densities across treatments within study areas and across all treatments were compared by One-way ANOVA; pairs of treatments were compared with t-tests. Within year comparisons of new seedling densities were not possible because of small numbers and missing treatments. Single treatment comparisons across years and multiple treatment comparisons across years were made with the non-parametric Friedman Two-way ANOVAs on untransformed data, and paired comparisons between adjacent years were made with the non-parametric Wilcoxon Matched-pairs Signed-ranks tests on untransformed data. For each study area for each year, we computed a weighted mean regeneration density, based on all

treatments; these were used in some of the regression analyses below..

We compared cone production within each transect among years from 1989 to 1994 using Friedman Two-way ANOVA. In order to determine whether a relationship existed between some measure of precipitation and density of new regeneration, we performed Pearson correlation analyses between various measures of precipitation and the weighted mean yearly regeneration for a study area; also, we examined the correlation between yearly new seedling densities within a treatment and a measure of precipitation. These correlation analyses were exploratory and not statistically rigorous: the regeneration densities for each year within a treatment are not strictly independent, and the number of data points ($n = 6$) is small. Nonetheless, they indicated trends.

Results

Verification of treatment designation

The composition of the pre-fire forest generally supported our designation of moist and dry ecological treatments, assuming no bias in the distribution of unidentifiable trees (Figs. 2 and 3). In dry treatments, fewer than about 14% of the trees were Engelmann spruce, and in moist treatments, 13% or greater (up to 85%) of the trees were Engelmann spruce . We obtained one anomalous result for the Mt. Washburn moist, moderately burned treatment: in one quadrat spruce accounted for 85% of the identifiable trees but in the second quadrat, only for 1% of the identifiable trees. In this second quadrat, however,more than 36% of the pre-fire trees could not be identified and another 36% of the trees were lodgepole pine.

Whitebark pine was not present in both quadrats from the Henderson Mountain moist, burned treatments or in one quadrat from the Mt. Washburn moist, burned treatment. In the

Henderson Mountain study area, subalpine fir dominated the pre-fire forest in all treatments, whereas in the Mt. Washburn study area, lodgepole pine and subalpine fir co-dominated in the dry treatment, with Engelmann spruce an additional co-dominant in the moist treatments.

Patterns of cone production and seedling germination over time

Whitebark pine cone production on the Republic Creek transect was moderate in 1989, the fall before the first summer of our study, and highest in 1991 (Fig. 4a). In 1992 the cone crop was poor, and virtually no cone production occurred in 1990, 1993, and 1994. Our observations of cone production in unburned forest on Henderson Mountain and in the adjacent Miller Creek drainage corroborate these findings. Republic Creek transect cone production differed significantly from 1989 to 1994 (Friedman Two-way ANOVA, $x_r^2 = 35.1$, $k = 6$, $N = 10$, $P = 0.000001$).

Cone production on the two Mt. Washburn transects showed similar patterns (Fig. 5A). The highest cone production for both transects occurred in 1989 and the lowest production in 1990 and 1994. Cone production was moderately high in 1991, moderate in 1992 and poor in 1993. From 1989 to 1994, yearly production differed significantly for both Transect 1(Friedman Two-way ANOVA, $x_r^2 = 46.2$, $k = 6$, $N = 10$, $P = 0.000000$) and Transect 2 ($x_r^2 = 36.5$, $k = 6$, $N = 10$, $P = 0.000001$). Comparing between both study areas, we find noteworthy similarities: good cone production in 1989 and 1991 with some production in 1992 and little to no production in 1990, 1993, and 1994.

In the Henderson Mountain study area, only the moist, unburned treatment had any new whitebark pine seedlings in 1990 (Fig. 4B). The burned treatments had no new or old whitebark pine regeneration in the first summer of the study. Not until 1991, however, did plots on three of

the four treatments show moderate densities of germinants; the dry, unburned treatment was the exception. Three treatments in 1992 had small numbers of new seedlings; this year, the moist, unburned treatment had no new regeneration. In 1993 all treatments experienced new regeneration, although the numbers were low for the moist, unburned treatment. In 1994 all treatments again had some new germination, but the dry, unburned treatment, which had not produced any new seedlings until 1992, had a relatively high density of germinants. None of the treatments had new regeneration in 1995.

For the Mt. Washburn study area, no new regeneration appeared on any of the treatments in 1990 (Fig.5B). Only the moist, moderately burned treatment supported patches of understory, which included a few older whitebark pine seedlings predating the fire. In 1991, all treatments experienced their first whitebark pine regeneration. In 1992 there was sparse germination on the dry, burned treatment and moderate numbers on the moist, moderately burned treatment. All three treatments had some germinants in 1993, with the moist, burned treatment showing great numbers (a conservative estimate). Again, in 1994 all treatments had low to moderate numbers of new seedlings, and in 1995, the two moist treatments again produced new regeneration.

The weighted mean regeneration densities for each study area (see also Fig. 4B and 5B) clearly indicate that 1991 and 1993 were major years for new whitebark regeneration in both study areas (Table 2).

There were some similarities in patterns of regeneration between the two study areas. Despite moderate to good cone production in 1989, 6 of the 7 ecological treatments experienced no germination in 1990. There was virtually no cone production in both study areas in 1990 but good to moderate germination on 6 treatments in the following growing season. Following good

to moderate cone production in 1991, 5 of the treatments produced low to moderate numbers of germinants in 1992. In 1993, all 7 treatments had new regeneration. Although cone production in 1993 was low, new germinants occurred in all 7 treatments in 1994. With no cone production again in 1994, there was still new regeneration on the two moist treatments in the Mt. Washburn study area in 1995. Thus, patterns of germination throughout the study were not predictable from patterns of cone production.

Comparisons of regeneration across ecological treatments and years

We examined the distribution of new regeneration density among the treatments (rows) and across years (columns), using Friedman Two-way ANOVAs. For all 7 treatments, the distribution across years differed significantly ($x_r^2 = 18.1$, $k = 6$, $N = 7$, $P = 0.0028$). We compared the distribution of regeneration across all 7 treatments two years at a time: the regeneration in 1991 was significantly greater than that in 1990 (Wilcoxon Matched-pairs Signed-ranks test, $z = 2.20$, $N = 7$, one-tailed $P = 0.0138$) and that in 1992 ($z = 2.20$, $N = 7$, one-tailed $P = 0.0140$) but other paired comparisons did not differ significantly. The distribution across years for the 4 treatments in the Henderson Mountain study area also differed significantly ($x_r^2 = 11.6$, $k = 6$, $N = 4$, $P = 0.0400$) but did not differ significantly for the 3 treatments in the Mt. Washburn study area ($x_r^2 = 8.95$, $k = 6$, $N = 3$, $P = 0.1110$). These results indicated greater year-to-year variation in seedling germination in the Henderson Mountain study area than in the Mt. Washburn study area. One major difference between the two areas was the absence of any new regeneration on Henderson Mountain in 1995 (Fig. 4b and 5b). For each of the seven treatments, the year-to-year variation in new seedling density was compared; the only significant difference among years occurred for the Mt. Washburn moist, burned treatment (Friedman Two-way ANOVA, $x_r^2 = 21.9$,

$k = 6$, $N = 50$, $P = 0.0005$).

We also examined among treatments the density of old regeneration, i.e., seedlings 1 to 5 years of age, that had survived to 1995. The highest and next highest old whitebark pine regeneration densities occurred on the Mt. Washburn moist, burned and moist, moderately burned treatments, respectively (Fig. 6). The lowest and next lowest regeneration densities occurred on the Henderson Mountain moist, unburned and Mt. Washburn dry, burned treatments, respectively. The density of old regeneration differed significantly among all 7 treatments (One-way ANOVA, $F_{6, 268} = 2.89$, $P = 0.0095$) and among the 3 Mt. Washburn treatments ($F_{2, 122} = 5.33$, $P = 0.0060$), but not among the 4 Henderson Mountain treatments ($F_{3, 146} = 0.80$, $P = 0.4945$). Among the Henderson Mountain treatments, there were no significant differences in old regeneration densities between the following treatment pairs: dry, burned vs. moist, burned; dry unburned vs. moist, unburned; dry, burned vs. dry, unburned; or moist, burned vs. moist, unburned. Among the Mt. Washburn treatments, the moist, burned treatment had a significantly greater old regeneration density than the dry, burned treatment ($t = -3.01$, $df = 98$, $P = 0.0017$) but the moist, burned and moist, moderately burned treatments did not differ significantly in density. We compared the Henderson Mountain and Mt. Washburn study areas and found that the dry, burned treatments did not differ significantly in old regeneration density; but, the moist, burned and moist, moderately burned Mt. Washburn treatments both had significantly greater densities of old regeneration than the moist, burned Henderson Mountain treatment ($t = -2.18$, $df = 98$, $P = 0.0157$, and $t = -1.80$, $df = 73$, $P = 0.0389$, respectively).

The relationship between moisture availability and new regeneration

The greatest numbers of new seedlings in both study areas appeared in 1991 and 1993. We investigated various measurements of moisture to ascertain any relationship between moisture availability and flushes of germination. Three measures of precipitation were selected: March plus April precipitation, mean monthly snow accumulation, March plus April mean snow accumulation, and total annual precipitation. For both study areas, we performed correlation analyses comparing each measure of precipitation against the weighted means for new seedling density from 1990 to 1995. (In almost all analyses, data did not depart from normality.)

For the Henderson Mountain study area, the only positive correlation obtained was between March plus April precipitation and weighted mean regeneration for each year of the study (Table 3), but the correlation was extremely low ($r^2 = 1.77\%$). We determined whether the effect might vary with burned and unburned treatments. In fact, the correlations improved for the dry, burned and moist, burned treatments ($r^2 = 9.90\%$ and 10.95%, respectively), but they were either strongly negative or small for the unburned treatments. A histogram of annual March plus April precipitation indicates that the greatest amount occurred in 1991 (Fig. 7a).

For the Mt. Washburn study area, by far the highest positive correlation with weighted means was obtained with March plus April precipitation ($r^2 = 44.38\%$) (Table 3). Given the small sample size, the high correlation is particularly noteworthy. For each treatment, there was also a strong, positive correlation. The histogram of annual March plus April precipitation clearly shows the greatest amounts occurring in 1991, 1993, and 1995.

Discussion

In this study, we demonstrated that the highest densities of whitebark pine seed germination did not follow moderate to good cone crop production, and that some germination occurred after virtually no cone production. For example, the two moist treatments in the Mt. Washburn study area exprienced new regeneration in 1995 (a year of high Marrch plus April precipitation), although there had been poor cone production for the preceding two years. Thus, delayed seed germination typically occurs in whitebark pine on both burned and unburned seed beds, at least in the Greater Yellowstone Area.

Moisture may play a limiting role in whitebark pine germination and survivorship in many parts of the species' range. In this study, the greatest cumulative whitebark pine regeneration occurred on the moist, burned and moist, moderately burned treatments on Mt. Washburn. These treatments were the most mesic of the study because of their northerly aspects; the moist treatments on Henderson Mountain were both southerly in aspect. In both study areas, the greatest densities of new seedlings followed years of high March plus April precipitation. Precipitation in these months may well determine soil moisture levels for the growing season. It is noteworthy that measurements of total annual precipitation or mean snow accumulation did not correlate well with whitebark pine regeneration.

The same traits that make whitebark pine seeds difficult to germinate under nursery conditions may prevent many newly-dispersed (and unretrieved) seeds from germinating during the next growing season and thus establish an adaptive moisture threshold. Seeds with underdeveloped embryos and endosperm may not be capable of germinating during the next growing season, and the physiological state of dormancy may reinforce this effect. The seed coat

may ensure that germination is initiated only in times with plentiful soil moisture. By germinating under favorable conditions, a seed has a higher chance of producing a surviving seedling.

The evolution of delayed seed germination in whitebark pine

Delayed germination in whitebark pine seeds is probably in part the consequence of seed dispersal by nutcrackers and in part the product of environmental selection pressures. First of all, the subalpine environment experiences a short season for growing and ripening cones. Nutcrackers begin to cache whitebark pine seeds in mid to late August. Those seeds cached early in the season may have more poorly developed embryos and endosperm than those seeds cached late in the season. In fact, August seed dispersal is exceptional among pines. Krugman and Jenkinson (1974) list the seed dispersal dates for 60 pines, not including subsection *Cembrae* pines. Of these, 55 pines disperse their seeds in September or later, and 5 pines disperse their seeds in August and September or from August to October: *P. armandii*, *P. monticola*, *P. ponderosa var. ponderosa*, *P. lambertiana*, and *P. strobus*. Of these five pines, *P. monticola* and *P. strobus* are known to experience delayed germination.

Delayed germination is known to occur in at least three of the five *Cembrae* pines, which are all nutcracker-dispersed: *P. albicaulis, P. cembra*, and *P. koraiensis*. This seed dispersal system may, in fact, favor the evolution of delayed germination as a "seed bank" strategy in these pines, which have good to moderate cone crops irregularly. Because nutcrackers cache seeds 2 to 3 cm in the ground, the seeds are less vulnerable to predators than wind-dispersed seeds and may maintain their viability for several years. This permits seeds the option of waiting for favorable conditions to germinate. By evolving moisture-resistant or impervious seed coats, the seeds can ensure that germination will not be triggered unless moisture levels are adequate. The result of

this syndrome of traits in whitebark pine seeds is 1) gerrmination under favorable conditions and 2) continuity of recruitment over time, in the absence of cone production.

We suggest that greater recruitment coming from this suite of seed characteristics may actually select for slow maturation in seed embryos and endosperm. In fact, if immature embryos did not increase recruitment levels, selection might speed development or delay seed coat maturation or cone ripening to discourage early caching by nutcrackers. In Table 4 we summarize the factors that may contribute to the evolution of delayed seed germination in whitebark pine.

We believe that the characteristics of whitebark pine seeds that lead to delayed germination are in part determined by taxonomic characteristics, by selection pressures in a high mountain environment, and, most importantly, by seed caching by nutcrackers. The long-term benefits to whitebark pine in terms of continual and, possibly, greater levels of recruitment from delayed germination should result in natural selection maintaining and enhancing these traits. A seed that germinates successfully and produces a seedling that reaches maturity and reproduces passes its traits to offspring. Lanner and Gilbert (1994) suggest that a major selective force favoring prolonged seed viability and delayed germination in whitebark pine is to provide a continual food supply in the form of ungerminated and germinated seeds to nutcrackers in between cone crops. Although it is possible that nutcrackers derive some nourishment from germinated and ungerminated seeds beyond the first growing season following dispersal and that helping to keep dispersers alive is indeed an indirect benefit from delayed germination, there are problems with this explanation as an evolutionary scenario. First of all, as in other seed dispersal mutualisms, the whitebark pine sacrifices a number of its propagules as food for nutcrackers in

exchange for disperser services. The issue is whether sacrificing propagules with the properties of delayed germination can favor the evolution of delayed germination in seeds. If a seed that has the characteristics that favor delayed germination is consumed, it cannot pass these traits on to offspring. The longer seeds delay germination, the fewer may germinate synchronously; nutcrackers searching for these germinating seeds may actually select against long delays in germination. It is also known that when whitebark pine cone crops fail, nutcrackers concentrate on alternative seed sources, such as ponderosa pine (e.g., Giuntoli and Mewaldt 1978). But more importantly, if delayed germination in whitebark pine seeds does, in fact, lead to greater recruitment through time for parent trees, then that in itself is a powerful and sufficient evolutionary mechanism for this phenomenon.

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Table 1. Ecological treatments for monitoring whitebark pine regeneration in the Henderson Mountain study area, Gallatin National Forest, Montana, elevation 2680 to 2745 m, and in the Mt. Washburn study area, Yellowstone National Park, elevation 2560 to 2745 m.

Treatments	Number of plots	Aspect
Henderson Mountain		
Dry, burned	50	80 - 180^0
Moist, burned	50	90 - 180^0
Dry, unburned	25	80 - 180^0
Moist, unburned	25	80 - 180^0
Mt. Washburn		
Dry, burned	50	270 - 290^0
Moist, burned	50	280 - 360^0
Moist, moderately burned	25	250 - 340^0

Table 2. Weighted means for new whitebark pine regeneration in the Henderson Mountain and Mt. Washburn study areas from 1990 to 1995. The means in the Henderson Mountain study area are based on four ecological treatments, and the means in the Mt. Washburn study area are based on three ecological treatments. See Table 1 for plot numbers within each treatment.

Year	Weighted mean density	
	Regeneration sites/m^2	
	Henderson Mountain	**Mt. Washburn**
1990	0.001	0
1991	0.014	0.020
1992	0.001	0.005
1993	0.013	0.019
1994	0.008	0.006
1995	0	0.005

Table 3. Pearson product-moment correlation analyses for 1990 to 1995 between 1) different measures of precipitation and weighted means for new regeneration in each study area and 2) March plus April precipitation and new regeneration in each ecological treatment.

y	x	r	r^2
HENDERSON MOUNTAIN			
Wt. mean regen.	Mar+Apr ppt.	0.133	1.77%
	Mean snopac	-0.503	25.26%
	MarApr sno	-0.376	14.16%
	Total ppt.	-0.369	13.64%
Dry, burned	Mar+Apr ppt.	0.315	9.90%
Moist, burned		0.331	10.95%
Dry, unburned		-0.723	52.24%
Moist, unburned		0.186	3.46%
MT. WASHBURN			
Wt. mean regen.	Mar+Apr ppt.	0.666	44.38%
	Mean snopac	-0.216	4.65%
	MarApr sno	0.089	0.79%
	Total ppt.	0.205	4.20%
Dry, burned	Mar+Apr ppt.	0.494	24.38%
Moist, burned		0.629	39.51%
Moist, mod burned		0.459	21.09%

Table 4. Factors contributing to the occurrence of delayed seed germination in whitebark pine and the evolution of a recruitment strategy based on seed dormancy.

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1. **Seeds require adequate moisture for germination.**
    - moisture-resistant seed coat
    - moisture threshold for germination
2. **Nutcrackers cache seeds.**
    - seeds remain viable in ground
    - decreased probability of predation
3. **Subalpine zone--short growing season.**
    - variation in seed embryo development
4. **Nutcrackers begin caching in August.**
    - seeds cached with immature embryos
5. **Cached seeds with immature embryos require more than one cold stratification period.**
6. **Adequate moisture triggers germination.**
    - better survivorship of seedlings
    - some seeds dormant in dry years
    - moisture threshold may vary
    - moisture varies with microsite
7. **Syndrome is adaptive:**
    - germination under favorable conditions
    - given intermittent cone crops, seeds can take advantage of favorable years
    - increased recruitment

8. Syndrome

- selects for moisture-sensitive seeds and late-maturing embryos
- results in (1) **germination under favorable conditions, and (2) continuity of recruitment over time**

Legends

Fig. 1. Map of Yellowstone National Park, Wyoming, indicating the location of the Henderson Mountain and Mt. Washburn study areas. Treatment locations are faintly outlined on the map.

Fig. 2. For the Henderson Mountain study area, the pie charts represent the distribution of conifer species in the pre-fire forest for each ecological treatment, as surveyed from a 30 m x 30 m quadrat. See text for details.

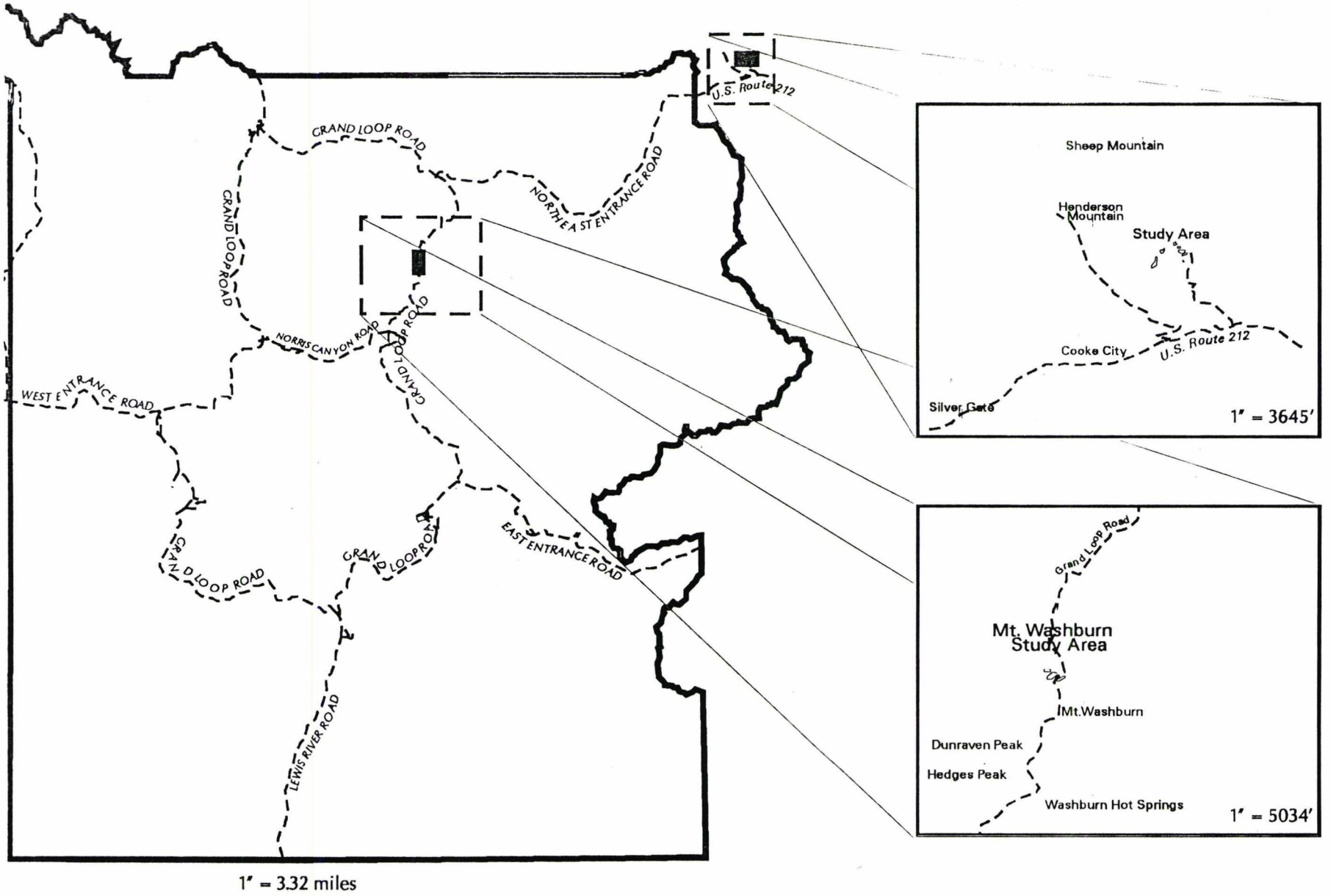
Fig. 3. For the Mt. Washburn study area, the pie charts represent the distribution of conifer species in the pre-fire forest for each ecological treatment, as surveyed from a 30 m x 30 m quadrat. See text for details.

Fig. 4. (A) Whitebark pine cone production on the Republic Creek Transect from 1989 to 1994. (B) Mean density of new whitebark pine seedlings (a single seedling or cluster of seedlings count as a single seedling site) for each ecological treatment in the Henderson Mountain study area for the summers of 1990 to 1995.

Fig. 5. (A) Whitebark pine cone production for Mt. Washburn Transects 1 and 2 from 1989 to 1994. (B) Mean density of new whitebark pine seedlings (a single seedling or a cluster of seedlings count as a single seedling site) for each ecological treatment in the Mt. Washburn study area for the summers of 1990 to 1995.

Fig. 6. The mean density of old whitebark pine regeneration (seedlings 1 to 5 years of age) that survived in each ecological treatment to be surveyed in 1995. Bars represent standard errors of the mean. A single seedling or a cluster of seedlings counted as a single seedling site.

Fig. 7. (A) Based on Fisher Creek SNOTEL data, March plus April precipitation for 1990 through 1995. (B) Based on weather data from the Tower Ranger Station, March plus April frozen and wet precipitation for 1990 through 1995. The data from the weather stations are not directly comparable; see text for details.

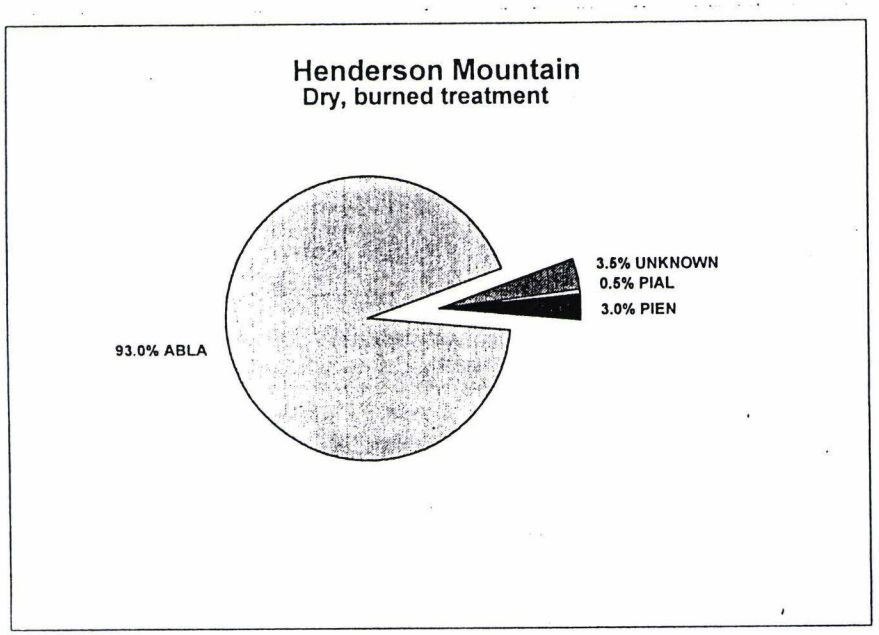


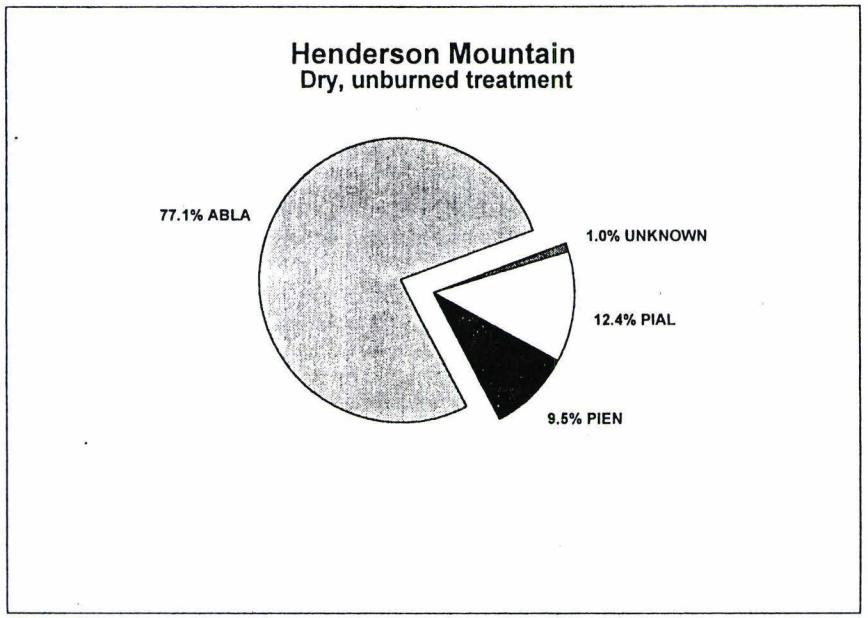
STUDY AREAS

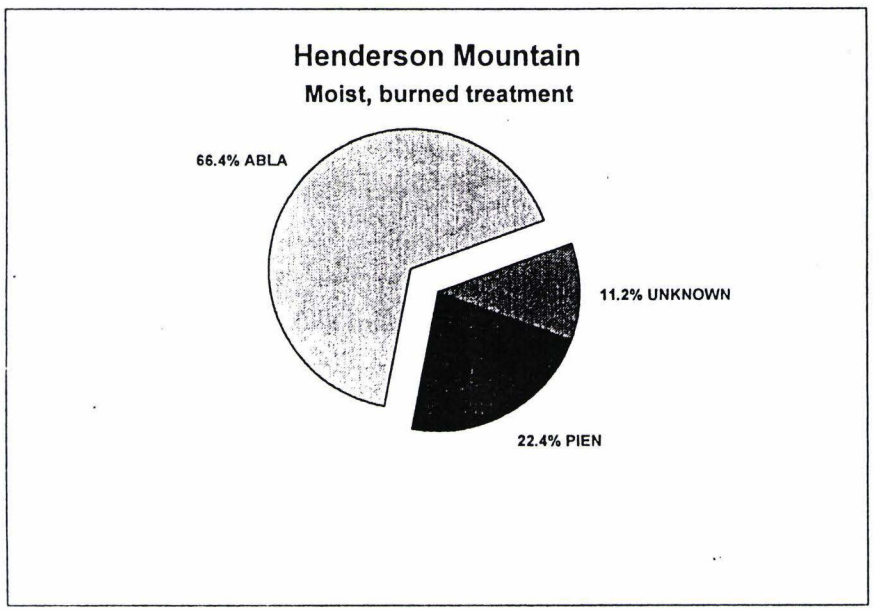
Park Border Roads Study Areas

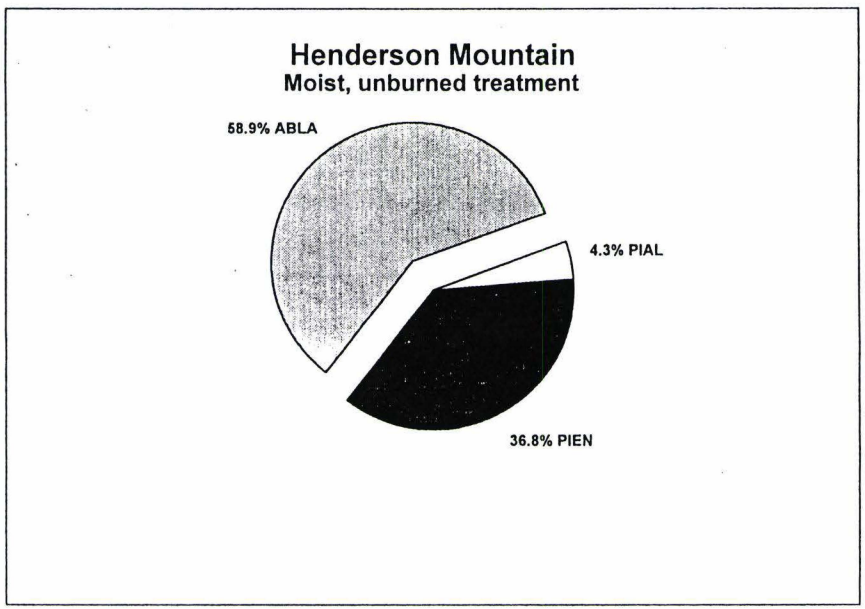
Study Sites

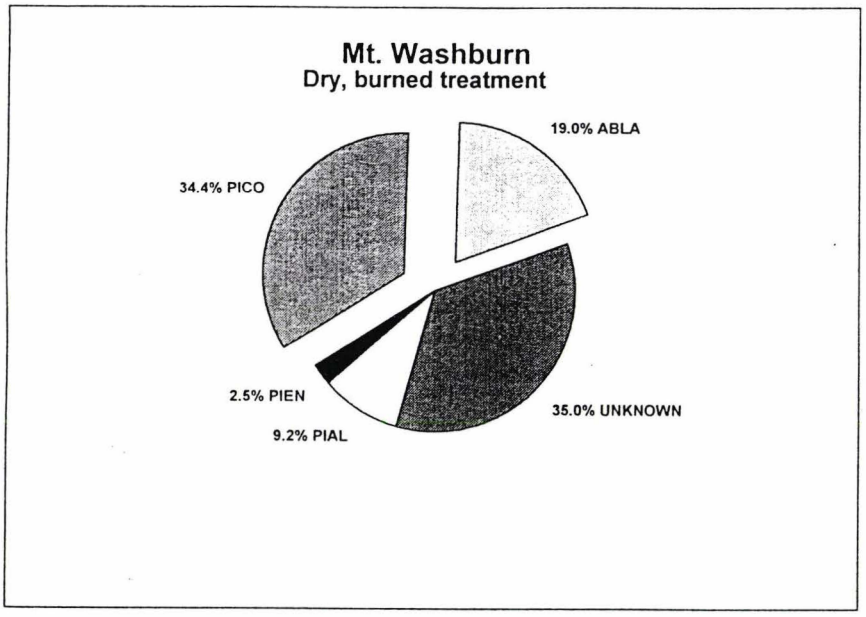
N
W
E
S

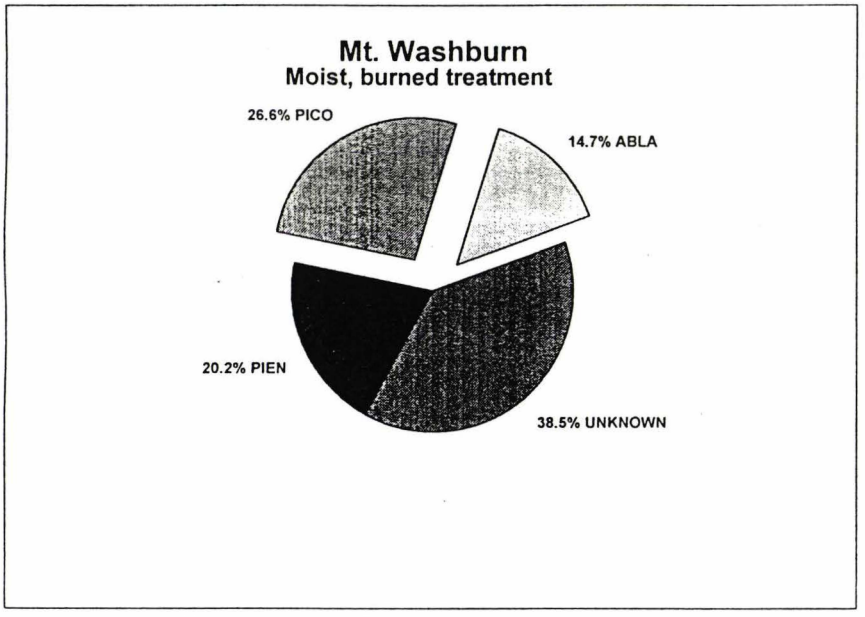

Henderson Mountain
Dry, burned treatment
93.0% ABLA
3.5% UNKNOWN
0.5% PIAL
3.0% PIEN

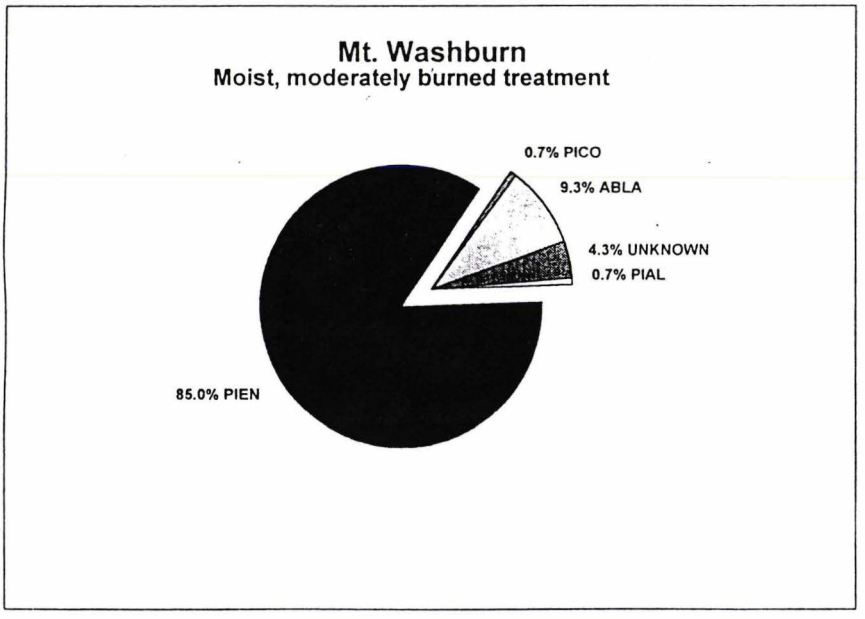

Henderson Mountain
Dry, unburned treatment
77.1% ABLA
1.0% UNKNOWN
12.4% PIAL
9.5% PIEN

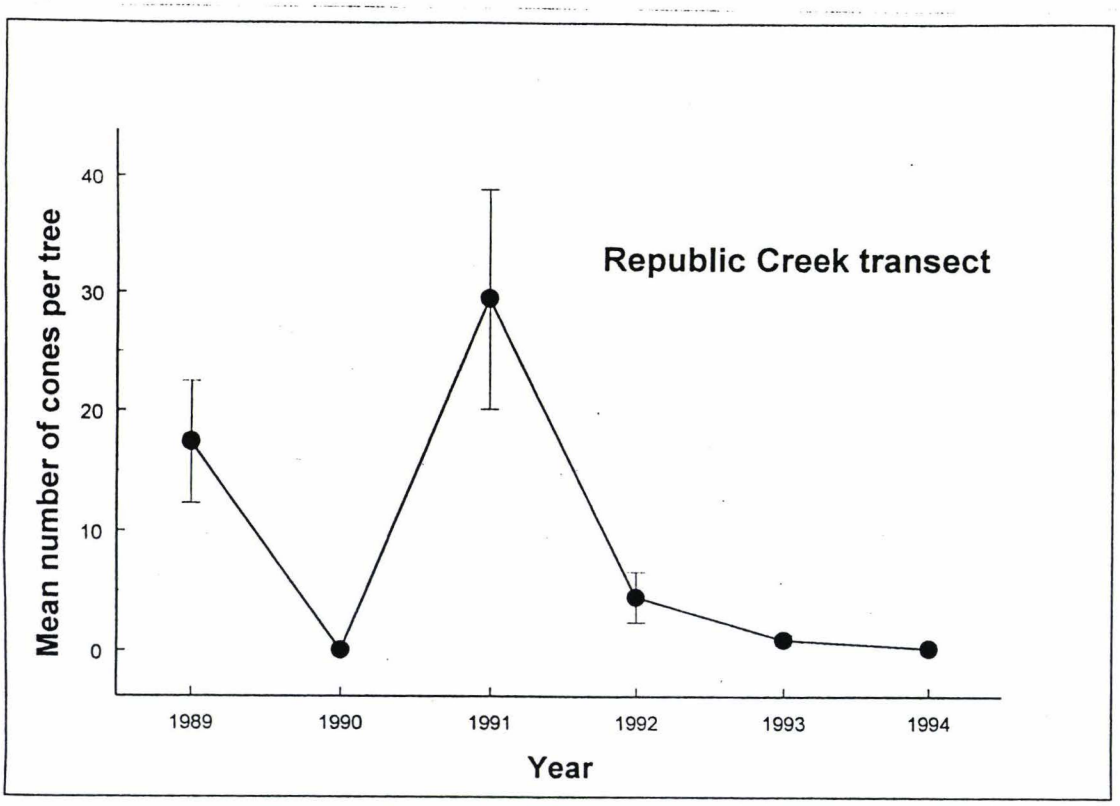

Henderson Mountain
Moist, burned treatment
66.4% ABLA
11.2% UNKNOWN
22.4% PIEN


Henderson Mountain
Moist, unburned treatment
58.9% ABLA
4.3% PIAL
36.8% PIEN

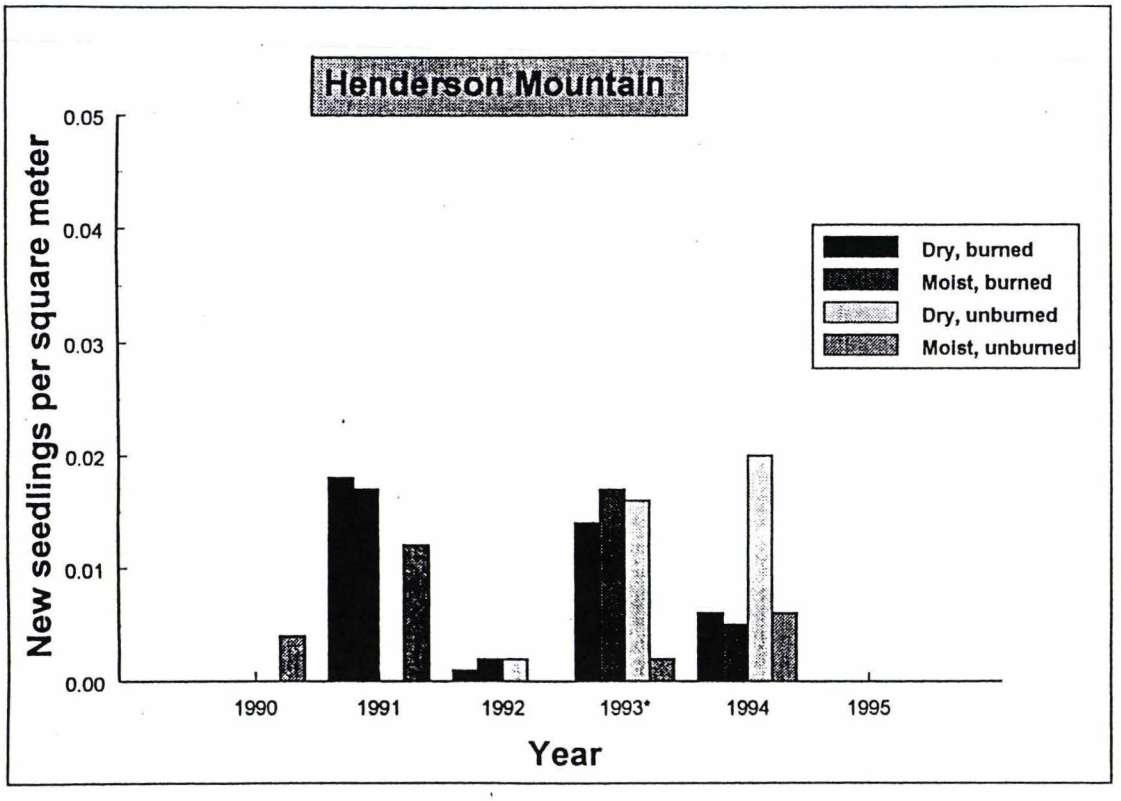

Mt. Washburn
Dry, burned treatment
19.0% ABLA
34.4% PICO
2.5% PIEN
9.2% PIAL
35.0% UNKNOWN


Mt. Washburn
Moist, burned treatment
26.6% PICO
14.7% ABLA
20.2% PIEN
38.5% UNKNOWN


Mt. Washburn
Moist, moderately burned treatment
0.7% PICO
9.3% ABLA
4.3% UNKNOWN
0.7% PIAL
85.0% PIEN

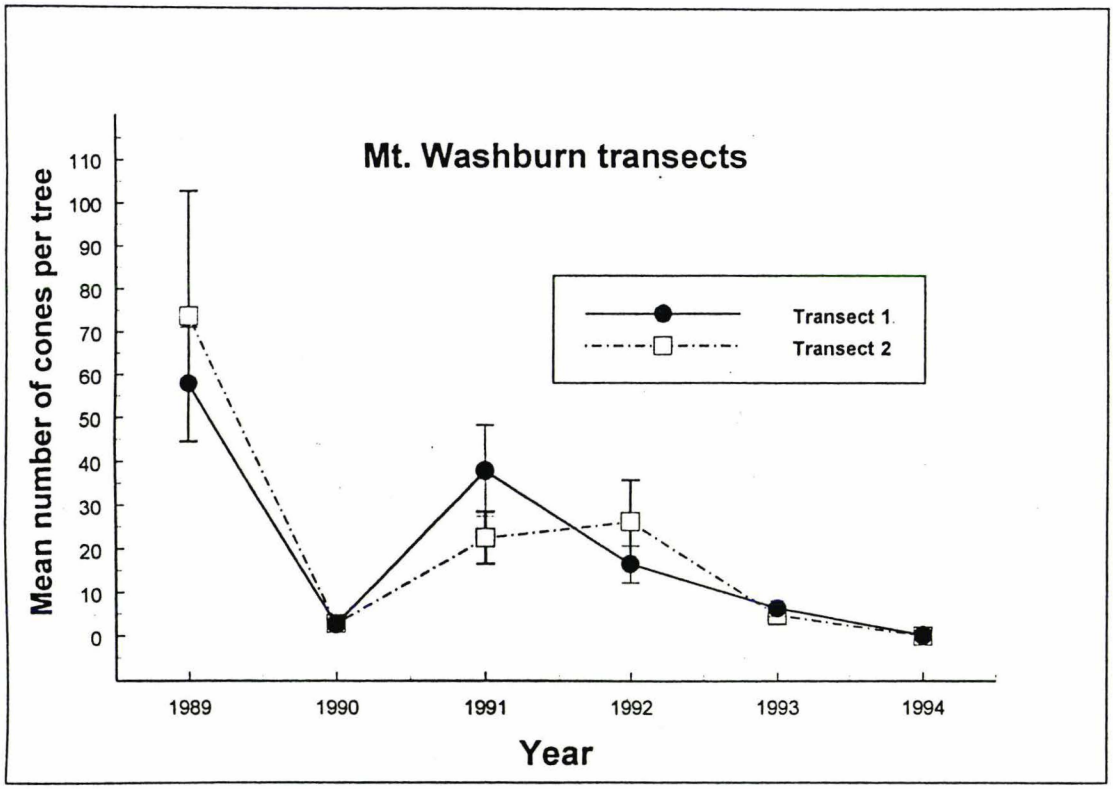

Republic Creek transect
Mean number of cones per tree
40
30
20
10
0
1989
1990
1991
1992
1993
1994
Year

A

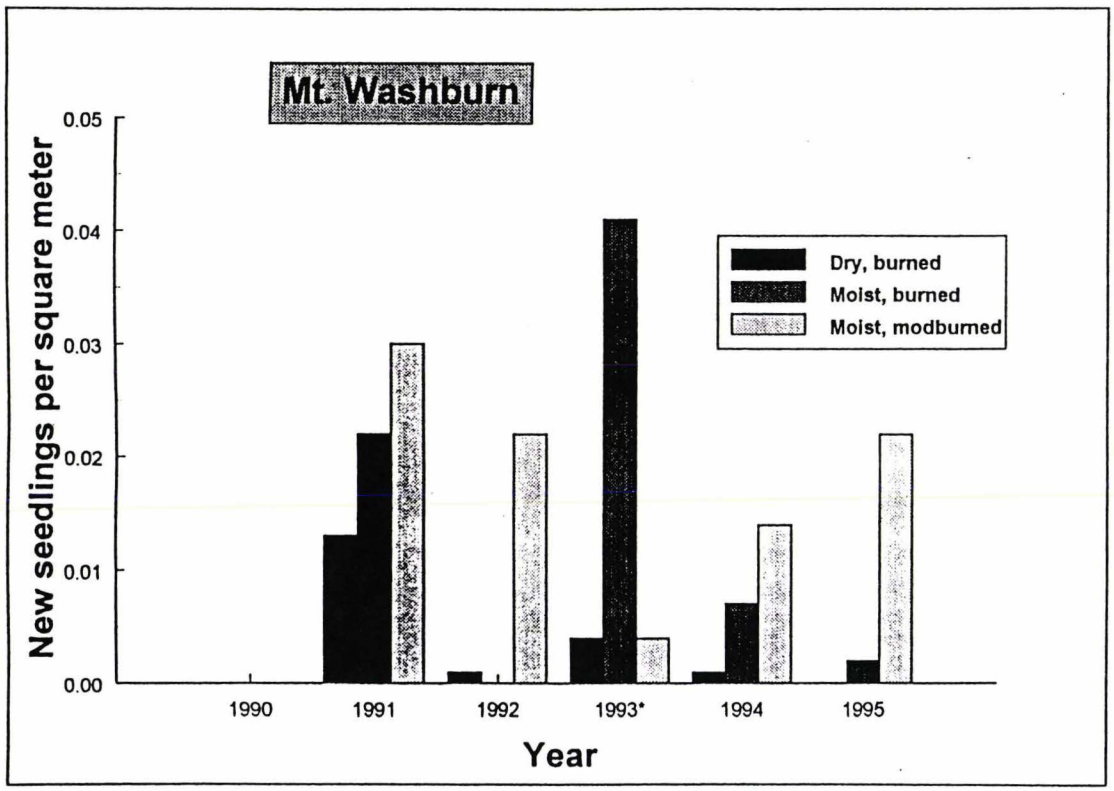

Henderson Mountain
New seedlings per square meter
0.05
0.04
0.03
0.02
0.01
0.00
Dry, burned
Moist, burned
Dry, unburned
Moist, unburned
1990
1991
1992
1993*
1994
1995
Year

B

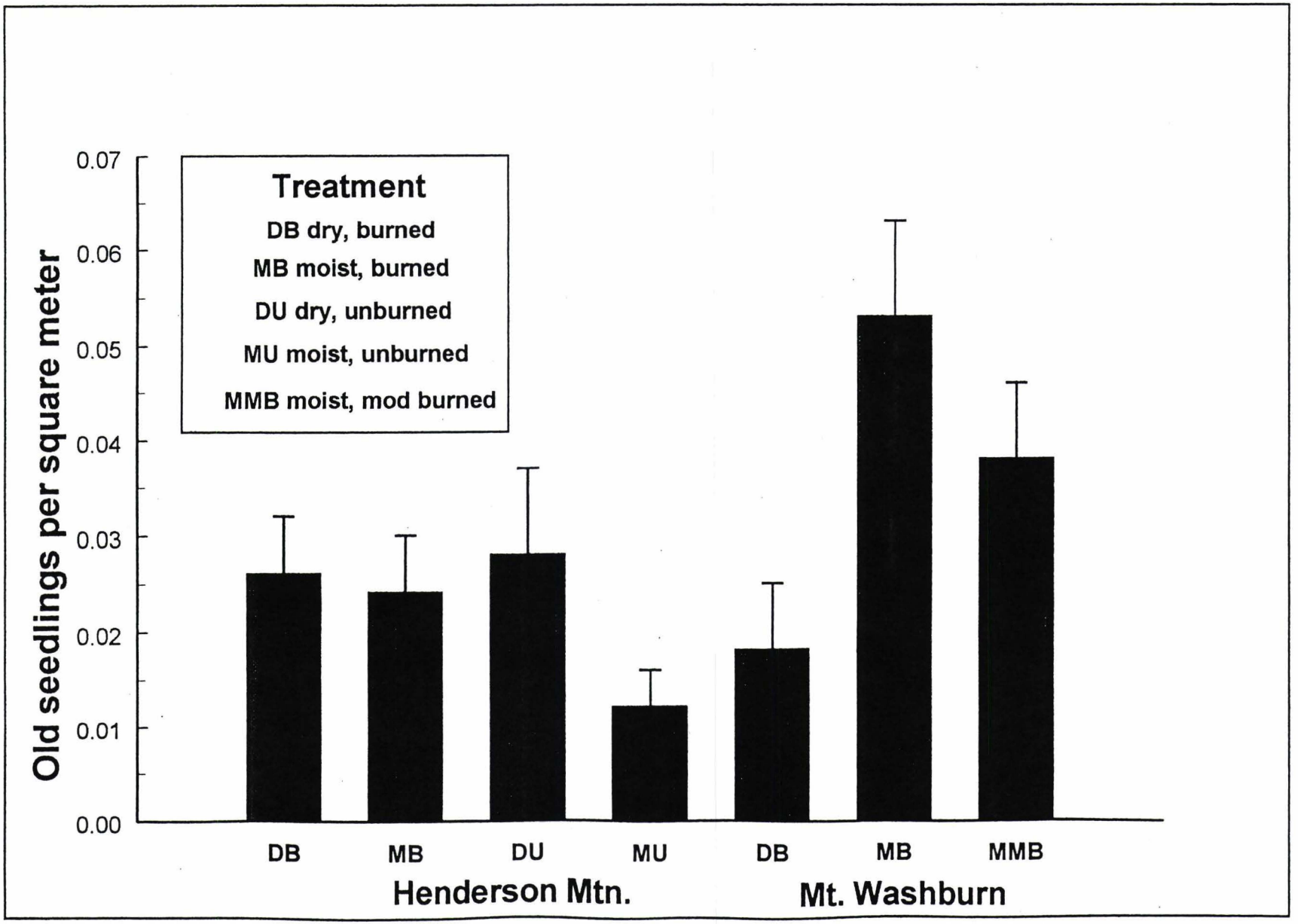
Fig 4

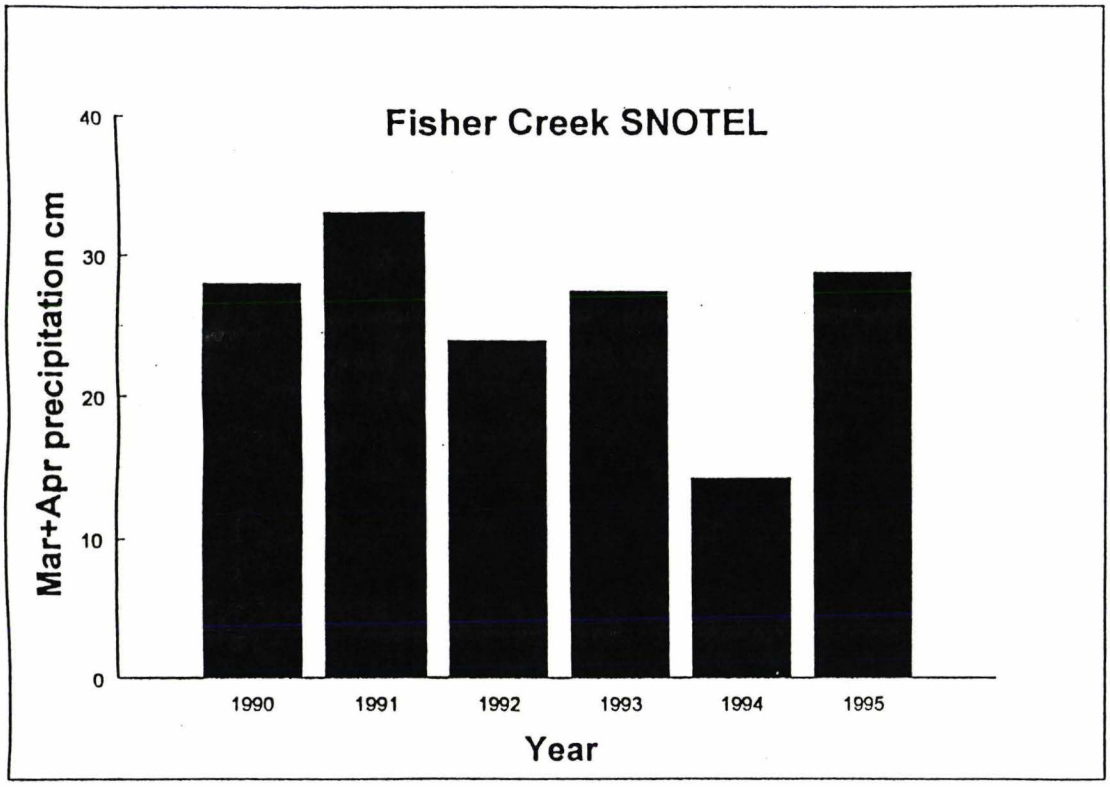

Mt. Washburn transects
Mean number of cones per tree
110
100
90
80
70
60
50
40
30
20
10
0
Transect 1
Transect 2
1989
1990
1991
1992
1993
1994
Year

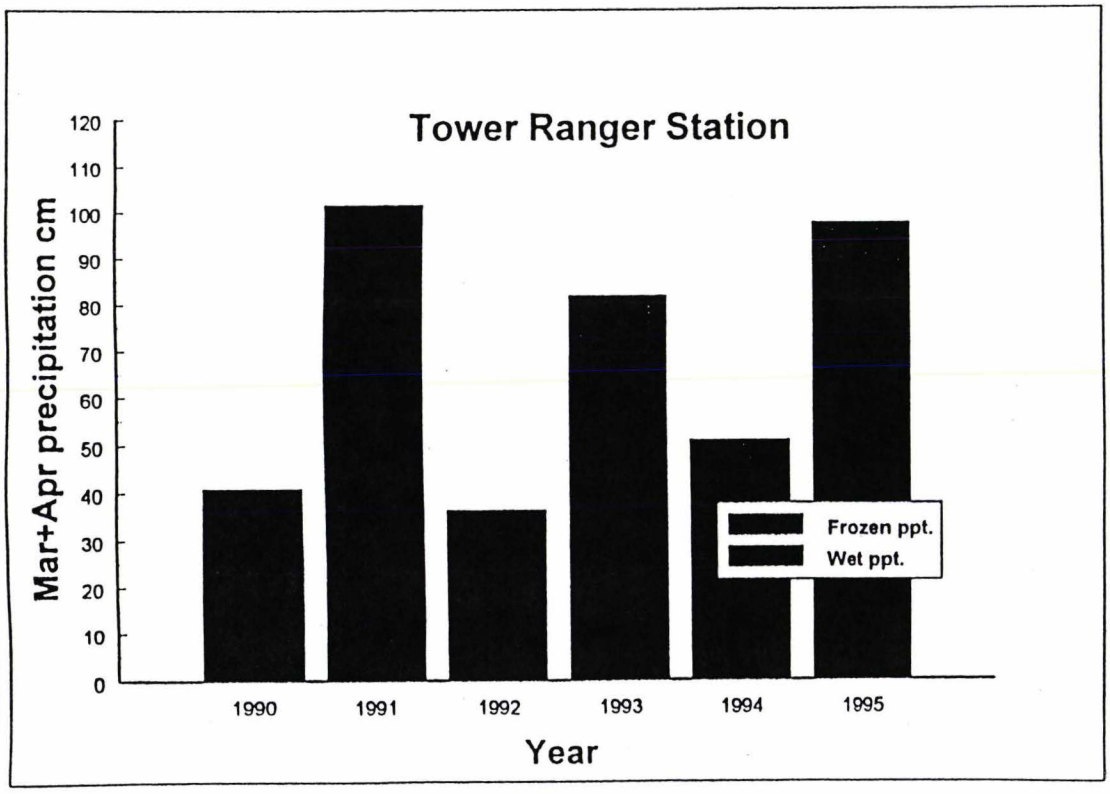
A


Mt. Washburn
New seedlings per square meter
0.05
0.04
0.03
0.02
0.01
0.00
Dry, burned
Moist, burned
Moist, modburned
1990
1991
1992
1993*
1994
1995
Year

B


Treatment
DB dry, burned
MB moist, burned
DU dry, unburned
MU moist, unburned
MMB moist, mod burned
Old seedlings per square meter
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
DB
MB
DU
MU
DB
MB
MMB
Henderson Mtn.
Mt. Washburn


Fisher Creek SNOTEL
Mar+Apr precipitation cm
40
30
20
10
0
1990
1991
1992
1993
1994
1995
Year


Tower Ranger Station
Mar+Apr precipitation cm
120
110
100
90
80
70
60
50
40
30
20
10
0
1990
1991
1992
1993
1994
1995
Year
Frozen ppt.
Wet ppt.